AMERICAN MUSEUM NOVITATES

Number 816 Published by THE AMERICAN MUSEUM OF NATURAL HISTORY New York City August 16, 1935

56.9, 81P (1181:78.8)

THE TIFFANY FAUNA, UPPER PALEOCENE

II.—STRUCTURE AND RELATIONSHIPS OF *PLESIADAPIS*

BY GEORGE GAYLORD SIMPSON

In 1854 Charlesworth gave the name *Platychoerops richardsonii* to a fragmentary palate from the London Clay, and in 1865 Owen renamed the same specimen *Miolophus planiceps*, and considered it as a relative of the hyracotheres. It was, in fact, a primate, the first discovered member of a very strange and primitive group, but its affinities were not recognized, even approximately, until Teilhard rescued it from oblivion in 1921, sixty-seven years after its first description. In the meantime a still older animal of closely similar character had been found at Cernay, near Rheims, by Lemoine, on whose first specimens Gervais based the genus and species *Plesiadapis tricuspidens* in 1877. Lemoine later described many additional specimens discovered by him. As a result of his work, most of the dentition was made known.[1]

Stehlin, in 1916, gave some much more satisfactory figures of *Plesiadapis* teeth from Cernay, and also named a new very closely related form, *Chiromyoides campanicus*, from the same locality. Teilhard revised and refigured Lemoine's material in 1921, giving full and accurate data on all the parts of the commoner Cernay animal so far discovered and preserved. He also showed that *Platychoerops* is a close relative of *Plesiadapis*.[2] Meanwhile, in 1915, Matthew had described an American genus and species, *Nothodectes dubius*, from a fragmentary jaw, the relationship of which with *Plesiadapis* was not at first recognized. In 1916 Granger, collecting in the beds later named Tiffany, in southwestern Colorado, found a small pocket of bones, the Mason Pocket, which proved to include remains of "*Nothodectes*" (*Plesiadapis*) as the commonest genus. In 1917 Matthew described the dentition as revealed by these specimens, then noting the close similarity to, and possible identity with, *Plesiadapis*. Teilhard (1921) considered *Nothodectes* as definitely synonymous with *Plesiadapis*, and in this all later students follow him.

[1] He also mentioned a number of skull and skeletal parts, but, except for the distal end of the humerus, these either proved to belong to other genera or were lost without having been adequately described.

[2] He considered them as identical, but in this I cannot follow him.

Matthew mentioned the existence of more and better material than he described in 1917, including parts of the skeleton, but preparation was not then completed and description was deferred. Gregory (1920) again mentioned the existence of this material, and briefly described a humerus from it. A full description, however, has never appeared.

In reviewing and more fully describing the Tiffany fauna, Doctor Granger's kindness in turning this invaluable collection over to me for study gave me the opportunity of preparing a description of all specimens of *Plesiadapis gidleyi*. The material being so much more complete than for any other animal in the fauna, its consideration overbalances the remainder of the review of the Tiffany fauna, and it is accordingly published as a separate part of the revision. All the morphological data and discussion of affinities are here presented. The minor points of differences between *Plesiadapis* and related genera (*Pronothodectes*, *Chiromyoides*, and *Platychoerops*) and the diagnosis of the several known species of *Plesiadapis* are given in the next (last) section of the Tiffany revision.

Unless otherwise noted, the following description is based on *Plesiadapis gidleyi*, which seems to be fairly representative of the genus and is incomparably the best known species. No part is known in another species and unknown in *P. gidleyi*, so that this description of the latter is nearly exhaustive of present knowledge of the genus as a whole.

MORPHOLOGY

DENTITION.—The dentition of *Plesiadapis* is already very well known from the detailed descriptions of the European specimens by Lemoine (various papers, see reference), Stehlin (1916), and Teilhard (1921), of many of the present specimens by Matthew (1917), and of other American species by Jepsen (1930). The teeth will therefore not be redescribed in detail, but a few additions and observations on obscure points or differences of interpretation must be made.

Matthew mentions a minute and doubtful vestige of an incisor anterior to the enlarged upper incisor, but it seems to me too doubtful to have any positive value. The enlarged tooth may be either I^1 or I^2. As Matthew stated, the maxillo-premaxillary suture is indeterminable, but his belief that there are two incisors followed by a canine seems highly probable and is in part confirmed by a bone fragment with the first two teeth, Amer. Mus. No. 17404, which appears to be a disarticulated premaxilla.

In two specimens, P^2 has a small and low but distinct inner cuspule

or incipient protocone, but on another (the type) this is absent, or represented only by a very slight basal swelling, and the whole tooth is relatively smaller.

The protoconule of P^{3-4} does not have the same structure as that of the molars. It is conical, not crescentic as in the molars, is closely applied to the paracone base, not well separated, and has no connection with the protocone-parastyle crest which passes anterior to it, not through it as on the molars. This and the absence of metaconule and mesostyle are the principal distinctions (aside from size and proportions) between P^{3-4} and M^{1-2}.

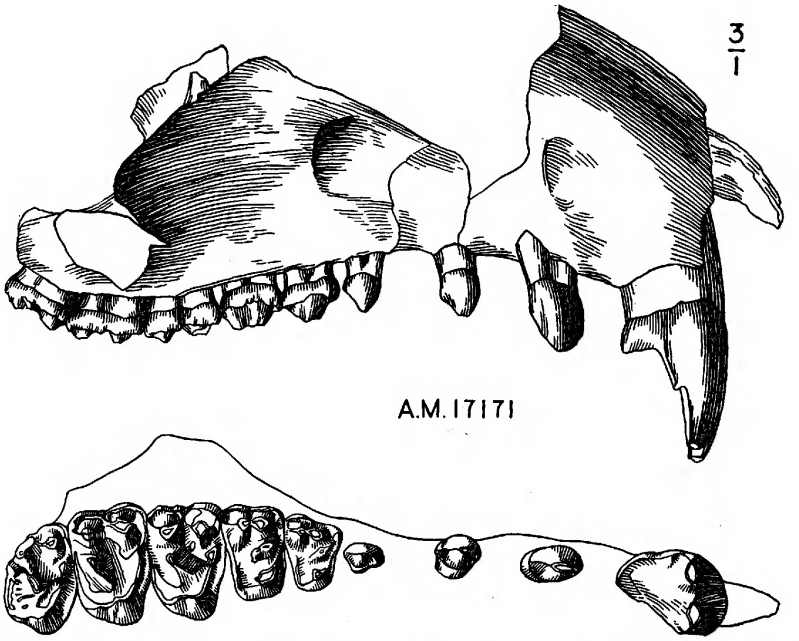

Fig. 1. *Plesiadapis gidleyi.* Right upper teeth, Amer. Mus. No. 17171. External and crown views. Three times natural size.

The upper molars have been very fully and accurately described.

P_2 is apparently absent in all other known species, but the alveolus is indicated in all specimens of *P. gidleyi* that show this region clearly. In the type the crown is present on both sides. It is exceedingly small, globular with an obscure apical pattern, and practically functionless although it is worn. As noted by Jepsen for another species, the flattened posterior faces of the protoconids of P_{3-4} bear three radiating ridges separated by two strong grooves. The heel of P_3 and that of P_4 are each

formed by a transverse crest, but the structure is slightly more advanced than this statement alone indicates. In both cases the crest bears two apices or cusps, and on P_4 another cusp, much smaller and variable, tends to appear between these. There is also a distinct tendency, especially on P_4, to enclose a heel basin by longitudinal lateral ridges, but these are always weak and the basin shallow.

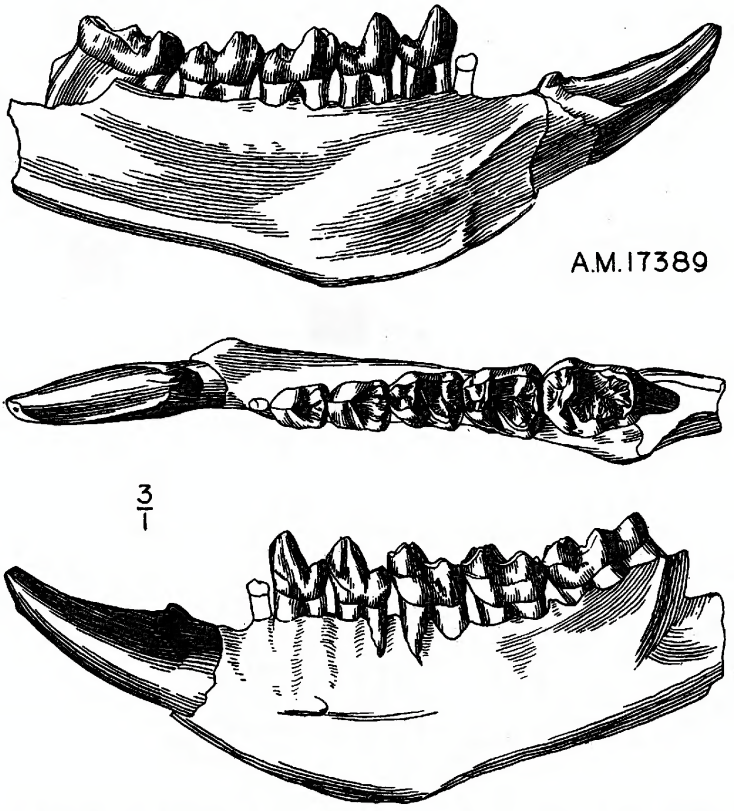

Fig. 2. *Plesiadapis gidleyi*. Left lower jaw, Amer. Mus. No. 17389. P_2, in outline, supplied from No. 17170. Internal, crown, and external views. Three times natural size.

On M_1 a shelf originates on the posterior side of the metaconid apex and passes obliquely down the flat posterior face of the trigonid to its base at the midline, where the shelf joins the hypoconid-trigonid crest. The latter crest reaches the trigonid at successively more external points on M_2 and M_3, and on these teeth the shelf alluded to apparently is quite absent even on unworn specimens. A constant feature of the trigonid is a deep short groove on the metaconid slope which falls into the trigonid

basin. Matthew (1917, p. 835) describes M_2 as having no paraconid but with "the metaconid . . . obscurely twinned, the posterior cusp having rather the relations of a metastylid." Teilhard (1921, p. 23) stated that in *Plesiadapis tricuspidens* the paraconid is distinct on M_{2-3} and suggested that in that species and also in *P. gidleyi* Matthew's metaconid is the paraconid, his metastylid the metaconid, and an obscure rudiment not mentioned by Matthew the incipient metastylid. Reviewing Matthew's material (which did not include all the Tiffany specimens, some being unprepared when he wrote), it is clear that he has described a morphological condition by giving his conclusion concerning its interpretation, rather than going into detail regarding the actual topographic details (a valid practise, in the interests of brevity, common in Matthew's work). The implied topography is the presence on M_1, but not on M_{2-3}, of the shelf described above, the fact that the inner trigonid cusps are much more nearly connate on M_{2-3} than on M_1, and the fact that on his specimens the anterior of these two cusps is or seems to be larger, the reverse of the usual condition among primates (and most other groups) when the paraconid is disappearing by fusion with the metaconids. On the least worn material (not seen by Matthew), however, the two cusps are generally of equal size or the posterior slightly larger. The posterior cusp has the essential characters of the metaconid of M_1, being united by a crest to the protoconid and bearing the groove on the trigonid side mentioned above. The probable metastylid rudiment mentioned by Teilhard is also distinctly visible on M_{2-3}, although only the faintest hint of it is seen on M_1 even when completely unworn. The homologies suggested by Teilhard are thus almost surely correct, although the topographic peculiarities implied by Matthew are present and very distinctive.

There is a distinct hypostylid on the hypoconid-trigonid crest, on M_{1-3} in *P. gidleyi*, made especially distinctive on M_3 by the presence of a notch, stronger than on M_{1-2}, between it and the hypoconid on the basin side of the crest. The talonid basins are not fully closed on any of the lower molars, the notch between entoconid and metaconid being open and almost as deep as the adjacent deepest part of the basin.

The talonid of M_3 is extended into a strong third lobe, as often described, but this is rarely or never as wide (does not extend so far externally) as the second lobe.[1] The hypoconid is distinct and separated by

[1] The tooth figured by Teilhard (1921) in his Plate I, fig. 11, is an apparent exception, but I cannot believe that this tooth belongs to *Plesiadapis*. Judging from the photograph, the third lobe is as long and wide as the second and larger than the first (trigonid), it is notched at the midline posteriorly, the trigonid is shorter than in *Plesiadapis*, and the internal trigonid cusp is either single or much less clearly double than in *Plesiadapis*. All these characters suggest *Phenacolemur* and the tooth may indicate the presence of an ally of that genus in the Cernaysian.

definite marginal notches from adjacent parts but the remainder of the talonid margin is essentially continuous, with an elevated rim on posterior and posterointernal sides. This is very obscurely divisible into cusps but generally a posteroexternal cusp and a slightly more anterior, lower, internal cusp (entoconid, which is thus part of the ridge and not distinct or opposite the hypoconid) can be distinguished. The rim between these may suggest a single elongate cusp or may itself be obscurely double. The enamel of the basin is highly rugose, even more so than on M_{1-2}.

Lemoine (1891, p. 280 and Pl. x, fig. 69*e*) described and figured a specimen with an unerupted permanent incisor, Dm_3, unerupted P_{3-4} and erupted M_{1-2}. His discussion goes no farther than to point out that there were three milk teeth in the lower jaw.[1] He also figured (Pl. x, fig. 70*s*) a tooth tentatively considered Dm_4. Its heel is so unlike that of Dm_4 in *P. gidleyi* that the reference is open to grave doubt.

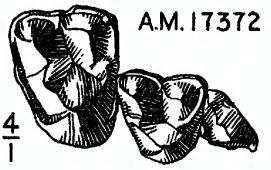

Fig. 3

Fig. 4

Fig. 3. *Plesiadapis gidleyi*. Dm^{3-4} and M^1, Amer. Mus. No. 17372. Crown view. Four times natural size.

Fig. 4. *Plesiadapis gidleyi*. Dm_{3-4}, Amer. Mus. No. 17372. Crown view. Four times natural size.

In the present material $Dm\frac{3-4}{3-4}$ are present in Amer. Mus. No. 17372, and there are three other specimens with milk teeth. Dm^3 has a triangular, sharp main cusp, on the posterior crest of which a minute metacone is visible. Parastyle and metastyle are both prominent, the latter larger. A very small posterointernal cuspule united by cingula to the two styles represents an incipient protocone. Dm^4 is fully molariform but of very different proportions from M^1, the length being nearly equal to the latter but the width little over half as great. The conules are relatively smaller, and the posterior cingulum is less expanded, although of identical structure otherwise.

Dm_3 is an elongate, triangular tooth. It has a minute rudiment of a metaconid, but the paraconid is suggested only by an angulation in the

[1] Only one was preserved, but from their unerupted condition he inferred, correctly no doubt, that the incisors and P_4 also had deciduous predecessors.

anterior crest. There is a small, basined bicuspid heel. Dm_4 is identical with M_1 in the general structure and relationship of all its cusps and crests but it is narrower throughout, the trigonid is narrower relative to the talonid, the trigonid is more elongate and triangular, and the paraconid is more distinct and projecting.

Dm^2 may possibly be represented in Amer. Mus. No. 17387 by an extraordinarily minute, one-rooted tooth with a blunt, formless crown, or termination. On this same specimen Dm^3 has the protocone still smaller than in Amer. Mus. No. 17372, the anterointernal cingulum absent, and no trace of a metacone. These are clearly individual variations.

SKULL.—Lemoine (1887, p. 190) briefly described skull parts from Cernay referred to *Plesiadapis* as follows: "C'est tout d'abord la plus grande partie d'une boîte cranienne indiquant une tête aplatie, plus large et moins longue que celle du *Pleuraspidotherium* et de l'*Orthaspidotherium*. La crête arrondie que surmonte l'occipital est fort développée et contraste avec le peu de saillie de la crête interpariétale. L'empreinte cérébrale se trouve bien conservée et indique l'égalité relative et l'indépendance des trois parties constituantes de l'encéphale: cerveau antérieur, cerveau moyen, cerveau postérieur ou cervelet. La surface du cerveau proprement dit du *Plesiadapis* paraît avoir été moins lisse que chez le *Pleuraspidotherium*. Deux autres fragments fournissent des indications sur la base du crâne et sur la constitution de l'oreille tant interne qu'externe, celle-ci largement ouverte au dehors."

This description is too general to be of any assistance in determining the affinities of the genus, and no later or more detailed data are available.[1] Teilhard (1921) did not find the specimens mentioned in the collection. It cannot be considered quite certain that they did belong to *Plesiadapis*, several skeletal elements described by Lemoine in the same paper having proved to be of other genera.

In the *P. gidleyi* material the palate, sides of the face, and a few basicranial characters can be made out.

The palate is long and of nearly equal width throughout. It is entire, even the anterior palatal foramina apparently being small, although not clearly shown. The choanae extended little, if at all, between the molars.

The zygoma arises opposite M_2 and beneath the orbit was expanded vertically (not horizontally as in *Tarsius* and so implying smaller orbits than in the latter), apparently deeper than in *Tupaia* and shallower than

[1] Osborn (1890), cited by Teilhard, gives only an abstract of this passage by Lemoine, and Schlosser's statements as to the skull are also wholly based on Lemoine.

in *Daubentonia*, much as in primitive lemurs. The infraorbital foramen is single and is above P_3. The face between this foramen and the anterior zygomatic rim is excavated. The lacrimal foramen is single, large, its canal diverted forward and downward, and it lies on the orbital rim near where the latter passes into the zygoma. It is thus marginal, but rather nearer being inside than outside the orbit. The lacrimal sutures cannot be surely made out, but the facial expansion was apparently small or absent. The lacrimal region appears to have been almost exactly as in *Notharctus* and *Adapis*. The distance between the bases of the median orbital walls is probably almost accurately shown in one specimen and is more than in *Tarsius*, less than in *Daubentonia*, and about as in generalized lemurs, again suggesting a moderate, lemuroid degree of orbital expansion without the peculiar structural lines of *Daubentonia*.

Much of the basicranium is present in Amer. Mus. No. 17388, but it has been crushed flat and broken into small disarranged fragments so that few characters can be determined. The pterygoid crest was evidently bifid as in tupaioids and primates generally, but its details are not clear enough to indicate any more specific resemblance, except that the somewhat distinctive type in *Daubentonia* is not indicated. The glenoid surface is flat with length and breadth about equal, and there is a small, discrete postglenoid process with a foramen at its inner edge, very much as in *Notharctus* and *Lemur* and less like *Tupaia*, *Tarsius*, or *Daubentonia*.

The bulla is completely ossified, but is remarkably small and relatively little inflated, less so than in any of the tupaioids or lower primates with which I am familiar. There was apparently no ossified external meatus. There are traces of the anterior lacerate foramen in its normal position and of closely approximated condylar and posterior lacerate foramina. The internal carotid almost certainly did not enter anywhere along the median side of the bulla, and there is evidence of a foramen at the posteroexternal corner of the bulla which is probably for this artery. So far as details of the ear region can be seen, they are not inconsistent with comparison with tupaioids, generalized lemuroids, or *Daubentonia*, but differ in the less expanded bulla and corresponding modifications. The general aspect is that of a small-bullaed *Notharctus*, but this may be superficial. The resemblance to *Tarsius* seems considerably more distant, but details are too few and too obscure for any very strong conclusion.

MANDIBLE.—The symphysis is unfused throughout life. In keeping with the rodent-like habitus, the straight cheek tooth series is implanted somewhat obliquely, so that the opposite rows are parallel. The symphysis is procumbent and inclined at about 30° from the horizontal,

more inclined than in *Daubentonia* and slightly less than in recent tupaioids. There is no mental prominence, but the deepest part of the jaw is at the posterior end of the symphysis, beneath P_{3-4}. Although more slender posterior to this point, the horizontal ramus is rather deep throughout. There are two mental foramina: one, larger, beneath the anterior root of P_3 and the other beneath the posterior root of P_4. Posterior to the molar region, the lower border of the mandible curves upward, then slightly downward again at the beginning of the angular process. This is a prominent, flattened, somewhat hooklike process curving backward and slightly downward. The condyle is far above the molar level and is moderately transverse, although its articular surface is

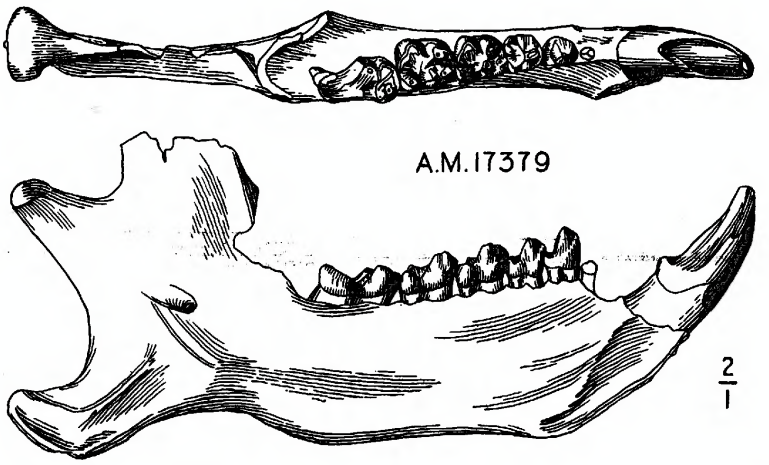

Fig. 5. *Plesiadapis gidleyi.* Left lower jaw, Amer. Mus. No. 17379. Superior and internal views. Twice natural size.

not cylindrical but rather evenly convex and mainly on the upper surface. The corono-condylar notch is deep and rather narrow. The coronoid is not completely preserved in any case, but clearly was high and broad anteroposteriorly. The base of the coronoid does not extend anterior to the middle of M_3. The masseteric fossa is broad and nearly flat, deep anteriorly and here bounded by stout, but not sharp, ridges. The inner surface of the posterior part of the mandible is nearly plane but has a prominent ridge along the lower border of the angle and extending forward and upward a short distance onto the horizontal ramus. On the angular process there is another small but sharp ridge above and parallel to this. The dental foramen is at the alveolar level but far posterior

to the alveoli. From its posteroinferior point a definite mylohyoid groove extends downward and forward.

With slight superficial differences correlated with the rodent-like habitus, the mandible as a whole resembles that of *Lemur* in basic type but differs somewhat from the lemuroids and decidedly from all other primates in the less broadened, more projecting angular process, in this feature being more like the tupaioids, which, indeed, it resembles throughout except for the rodent-like adaptive characters and the generally much heavier build. It is extraordinary that despite the somewhat similar adaptive dental type, the lower jaw is very unlike that of *Daubentonia* in almost every character.

VERTEBRAE.—The structure of the atlas is fully visible in Amer. Mus. No. 17379, and in every essential it agrees with *Lemur*. Indeed I see no character of this bone in *Plesiadapis* not exactly matched in one or another of the rather variable atlases of *Lemur* and its close allies, with the single possible exception of the cotylus, which in *Plesiadapis* has the long axis at a smaller angle from the horizontal and its upper outer portion is less concave, the lip less produced. Comparison with the lorisiforms, in which the atlas is quite distinctive from that of the true lemurs, is much less close and *Tarsius* also has a highly modified atlas different from this type. *Daubentonia* has a *Lemur*-like atlas, and to that extent is also like *Plesiadapis*, but the latter is closer to *Lemur* in exact details. The tupaioid atlas differs more from that of *Plesiadapis* than do either *Lemur* or *Daubentonia*.

Parts of the other cervicals are present in Amer. Mus. No. 17388, but aside from their having primitive primate general proportions, nothing definite can be made out.

In Amer. Mus. No. 17379 two mid-dorsals, six lumbars, the sacrum, and two anterior caudals are preserved and have been wholly freed from the matrix.

The two dorsals are closely similar save that one, presumably more anterior, has slightly longer transverse process. The centrum is longer than broad and broader than deep and has a single or vaguely double rounded ventral ridge with a prominent foramen in the concavity on each side. The transverse processes are pedunculate, with expanded ends. The neural notches are large and deep, reaching to the posterior edges of the transverse processes. The roof of the arch is very little elevated and is smoothly convex transversely. The zygapophyses are little differentiated from the arch. The articular surfaces of the postzygapophyses are very gently concave and face downward and slightly inward. Succes-

sive vertebrae of this region overlap dorsally like a series of scales. The neural spines are slightly broken, but probably they were short. Each is small and styliform, springs from the extreme posterior end of the arch, and is directed strongly backward, little upward. Of the types with which I have compared them, these vertebrae are definitely more like the lemurs,

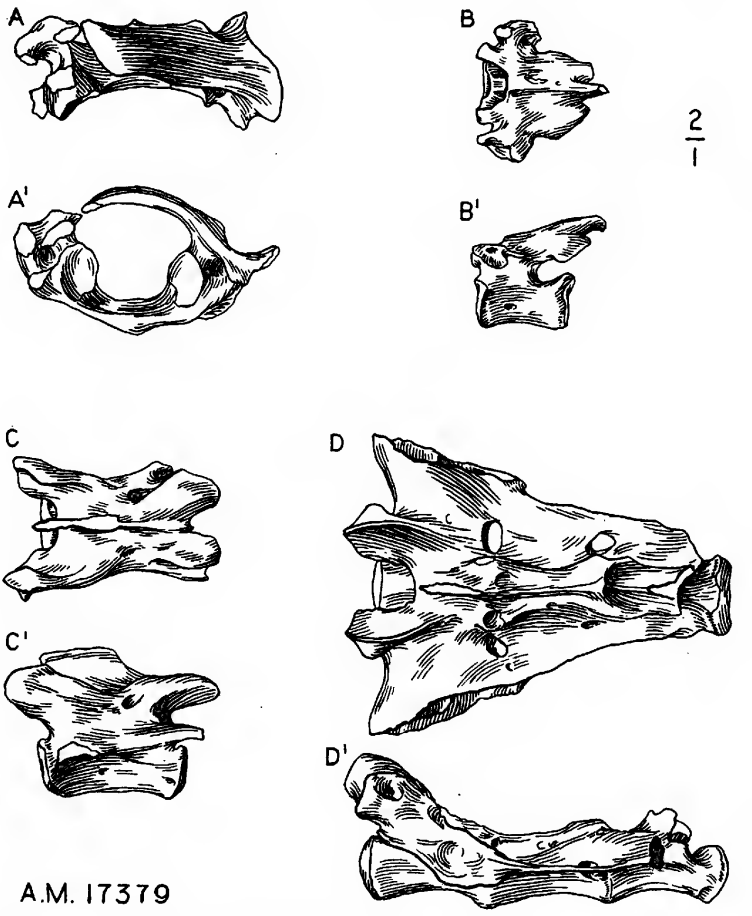

Fig. 6. *Plesiadapis gidleyi.* Parts of vertebral column, Amer. Mus. No. 17379. A dorsal, and A′ posterior views of atlas. B dorsal, and B′ left lateral views of dorsal vertebra. C dorsal, and C′ left lateral views of lumbar vertebra. D dorsal and D′ left lateral views of sacrum. All twice natural size.

but the transverse processes are slightly shorter and stouter (but figures of other lemur skeletons suggest that this is not true of all) and the neural spine markedly less erect in *Plesiadapis*. *Daubentonia* is equally different in these characters and also has quite different proportions, and

Tarsius is still more unlike the fossil. The vertebrae of *Tupaia* are similar to the extent that they are lemur-like.

Five of the six preserved lumbars differ chiefly in size, becoming larger posteriorly. The centrum in each case is elongate and moderately depressed. Its ventral ridge is broad and flattened on the more anterior and sharp on the more posterior lumbars. The more anterior vertebrae apparently had only slight swellings in the position of the transverse processes, but the more posterior have broken bases which probably supported small but projecting anterior tranverse processes. The neural notch is much shallower than on the dorsals. All six of these vertebrae have strong typically primate anapophyses, and the zygapophyses are well differentiated and also of normal, primitive primate type. The spine is adequately preserved in only one case, there being low, squarely truncated, long anteroposteriorly, and directed forward.

The other preserved lumbar was still more posterior and was probably the second (possibly the first) in front of the sacrum. It is still larger than the most posterior of the others, has a transverse process running the full length of the base of the neural arch (broken off on each side), no separate anapophysis, the spine shorter anteroposteriorly but more erect and probably higher.

These vertebrae are somewhat more strongly ridged ventrally than in *Lemur*, the spine is slightly different in shape, and there are other very minor differences but the general agreement is remarkably close. The distinctions (apparently not very important) between either *Tupaia* or *Daubentonia* from *Lemur* in this region are in each case equally distinctions from *Plesiadapis*, and *Tarsius* is quite definitely unlike *Plesiadapis*.

The sacrum is formed of three fused vertebrae, the first broadened and the others elongate, all with strongly depressed centra. The sacrum differs from that of *Lemur* chiefly in having the transverse processes of the first vertebrae longer and more flaring, elevated at the ends, the iliac scar more elongate and its long axis at a larger angle to the long axis of the sacral centra. The iliac articulation was almost entirely with the first vertebra (as in *Lemur*). The other transverse processes are somewhat broken.

The peculiarities of the tupaioid sacrum with respect to *Lemur*, such as the quadrate outline, reduction of the foramina between the transverse processes, or fusion of the spines, are all also distinctions from *Plesiadapis*. *Daubentonia* also differs in its non-*Lemur*-like characters, which are more numerous and definite than in *Tupaia*. *Tarsius*, however, is about as similar to *Plesiadapis* as is *Lemur*, but not more so.

The two anterior caudals are similar, but one has the centrum slightly keeled, the other not. These vertebrae are smaller than the posterior lumbars. Length and width of centrum are about equal, the depth much less. There were strong transverse processes (ends broken off). The neural arch is of the same type as that of the posterior lumbars, but smaller and with the zygapophysial facets farther from the vertical. There are small erect neural spines.

RIBS.—There are numerous rib fragments, but they show nothing of interest except that the ribs are slender and normal.

SCAPULA.—Part of a left scapula is associated with Amer. Mus. No. 17379. The parts preserved are almost exactly as in the tupaioids and Madagascar lemurs, the regions in which these very closely similar types differ not being preserved, except that the lower part of the prespinous fossa is wide, more as in tupaioids, and that the upper part of the postspinous fossa is concave and not flattened, more as in *Lemur*. The peculiarly rodlike type of *Tarsius* is not suggested. *Daubentonia* almost exactly resembles *Lemur* in these parts, except for the flattening of the postspinous fossa, a difference from the fossil.

HUMERUS.—The nearly complete right humerus of Amer. Mus. No. 17379 has already been figured and described by Gregory (1920, p. 70 and Pl. XXVII). He points out that this bone in *Plesiadapis* ("*Nothodectes*") differs from that of *Notharctus* as follows:

(1) The delto-pectoral crest is very thin and acutely V-shaped, as seen from the outer side, ending below in a prominent pointed tip.

(2) The supinator crest is not so large as it is in *Notharctus* and does not extend up to the level of the deltoid tip.

(3) The trochlea is relatively larger and more extended vertically.

(4) The tuberosity for the teres major, on the inner side of the shaft, is much larger and more sharply defined.

In place of (3) I would write:

(3) The trochlea has only a faint suggestion of the cylindrical form and outer lip typical of modern lemurs, *Notharctus* being approximately intermediate in this respect between the latter and *Plesiadapis*.

And I would add:

(5) The shaft as a whole is more curved and sigmoid.

(6) The entepicondylar foramen is more distal, nearer but more lateral to the trochlea.

With the exception of (2), which is a definite resemblance to modern lemurs, these are all also differences from *Lemur* and its allies.

The general habitus and curvature suggest *Tarsius*, but this is an adaptive feature and *Plesiadapis* has none of the special peculiarities of

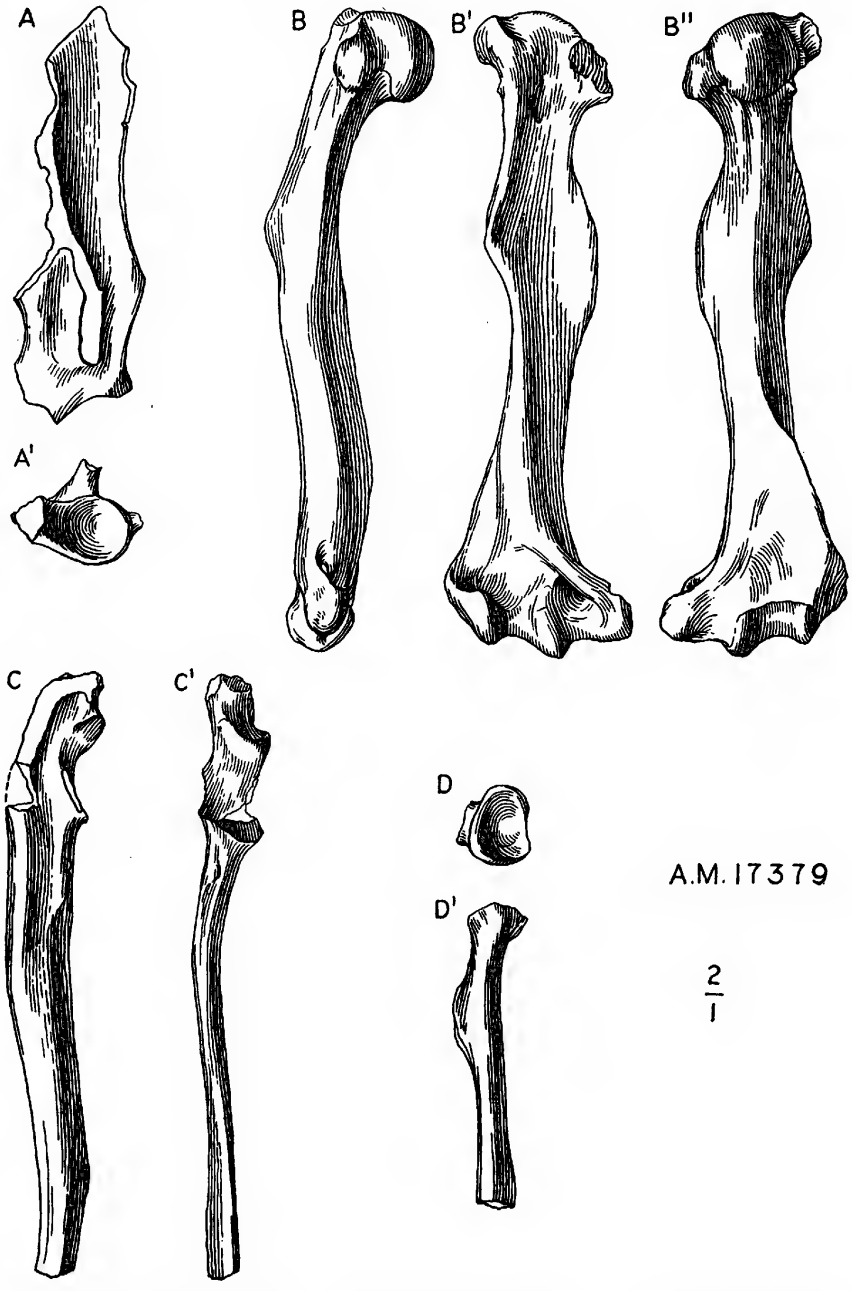

Fig. 7. *Plesiadapis gidleyi.* Parts of anterior limb, Amer. Mus. No. 17379. A lateral and A′ distal views of part of scapula. B internal, B′ anterior, and B″ posterior views of humerus. C internal and C′ anterior views of broken ulna. D proximal and D′ (approximately) internal views of part of radius. All twice natural size.

the *Tarsius* humerus, and it also lacks the peculiarities of *Daubentonia*, notably the specialization of the supinator crest, being more *Lemur*-like than either of these.

As Gregory notes, the humerus of *Ptilocercus* could be derived from that of *Plesiadapis*, but so could that of *Lemur*, and looking at the matter in a different way I do not see that the resemblance to *Ptilocercus* is specific, going beyond what could be expressed by calling both lemuroid. (1), (4), (5), and (6) are as unlike *Ptilocercus* as *Lemur*. In (2) *Plesiadapis* is more like *Lemur* than like *Ptilocercus*. In (3) *Ptilocercus* is a little like *Plesiadapis* in being slightly more primitive than is *Lemur* itself, but *Plesiadapis* is as near to *Notharctus* as to *Ptilocercus* in this respect. In résumé, it seems accurate to say that *Ptilocercus* closely resembles the lemurids in the humerus, that *Plesiadapis* resembles them also but less closely, and that the humerus of *Plesiadapis* is at least as much like that of lemurids as like that of any tupaioid. I therefore cannot share Gregory's opinion that the humerus of *Plesiadapis* gives evidence that the Plesiadapidae are tupaioids[1] and not lemuroids.

The humerus referred by Lemoine and doubtfully by Teilhard (1921, Pl. I, fig. 33) differs in the less produced entepicondyle and slightly larger and more proximal foramen, but could well be congeneric.

RADIUS.—The proximal half of the right radius is present in Amer. Mus. No. 17379. It differs from that of *Lemur* chiefly in having the fovea oval rather than circular and with its rim narrower and sharper and in lacking the pit on the neck above the tuberosity. The bone is broken just at this point, but there appears to have been an eminence for the pronator teres. This and the oval fovea are tupaioid characteristics, but the first is equally present in *Notharctus* and the latter suggested. In tupaioids the tuberosity is much weaker. In *Daubentonia* the head is circular and the tuberosity and pronator eminence are much weaker. *Tarsius* differs still more markedly.

ULNA.—Most of the left ulna, lacking the distal end, is preserved in the same specimen, and there is another fragment, the proximal end of a right ulna lacking the olecranon. The sigmoid notch is somewhat shallower and longer relative to its width than in *Lemur*, the proximal portion also somewhat larger relatively and more strongly curved (convex). All these characters are resemblances to *Notharctus*. As in *Lemur* but not in *Notharctus* a small crest separates the articulations for the humerus and for the radius. The olecranon is relatively a little shorter than in *Lemur*, but otherwise closely similar, as is the whole proximal end. As in

[1] "Menotyphla," but the comparison is with tupaioids.

Lemur, a sharp crest appears on the lateral side of the distal part of the shaft, but anterior (or interosseous) and posterior borders are also sharply crested here and the surfaces between the three crests are all concave. This differs from *Lemur* and also (but rather less) from *Notharctus*, but is rather closely approached in *Perodicticus*. The resemblance of the ulna as a whole to the tupaioids seems to involve only characters that are also lemurid, and to be somewhat more distant than to the lemurids. Exactly the same statement could be made substituting "*Daubentonia*" and "*Tarsius*" for "tupaioids." The bone, as preserved, has indeed a peculiar twist distal to the sigmoid notch which is also suggested in *Tarsius*, and not in the other forms compared, but this may be, and I think probably is, due to crushing.

METACARPAL.—In probable association with Amer. Mus. No. 17379 is a bone of appropriate size and structure to be a third or fourth meta-

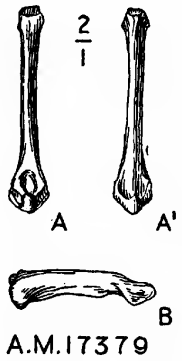

Fig. 8. *Plesiadapis gidleyi*. Foot bones, Amer. Mus. No. 17379. A dorsal and A′ palmar views of (?) metacarpal. B, lateral view of phalanx (probably of pes). Twice natural size.

carpal of *Plesiadapis gidleyi*. The proximal articulation is very simple, with the form of a truncated triangle, wider dorsally, convex in the dorso-palmar direction and plane transversely. The shaft is simple, slender, widening distally, and nearly circular in section. The distal end is very peculiar, of a type approached by tupaioids and primitive insectivores but not achieved, in specialization, in any form examined by me. A medial pit on the dorsal surface is followed distally by a spherical articular process which on the palmar side continues into two earlike posterolateral wings. There is also a short but prominent median palmar keel.

PELVIS.—The pelvis is not present in the best specimen, Amer. Mus. No. 17379, but Amer. Mus. No. 17409 is a nearly complete, isolated left half of a pelvis, lacking only the symphysis and a small part of the anterior end of the ilium, and almost certainly belongs to this species. There are also two other specimens, but they add little or nothing.

The ilium is rodlike and of moderate length. Near its midpoint, where the diameter is least, its section is markedly and almost equilaterally triangular, the superolateral face being 4.0 mm. in width, inferolateral 3.8, and medial 3.5, in one specimen, and in another 3.5, 3.4, and 3.4, respectively. More anteriorly, in the articular region, the superior face flares somewhat, but even here its greatest width (in the smaller specimen mentioned) is only 4.7 mm. while that of the inferior face is 3.6 mm. This relatively slight expansion of the superolateral face is a marked distinction from *Tupaia*, *Notharctus*, or lemurids, but more like the latter as they are the least expanded of the three groups, although still markedly more so than is *Plesiadapis*. *Daubentonia* is as little expanded

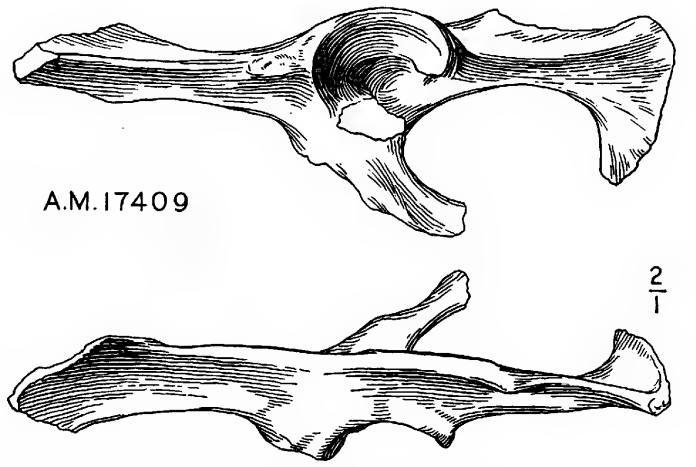

Fig. 9. *Plesiadapis gidleyi*. Pelvis, Amer. Mus. No. 17409. Lateral and dorsal views. Twice natural size.

as is *Plesiadapis*, but its ilium is nevertheless very different, the lateral face not being divided by a crest into superior and inferior parts, and the blade being of nearly equal width throughout and straighter than in *Plesiadapis*. The pelvis of *Tarsius* is so unlike that of *Plesiadapis* in all its distinctive details that comparison is unnecessary. The sacral scar is large and apparently the ilium was less extended anterior to it than in any of the genera used for comparison, but this is uncertain due to the poor preservation of this part in the specimens.

It seems to be a lemurid character, as opposed to tupaioids, higher primates, or even *Daubentonia*, that the angle between the sacral and iliac axes is small. This cannot be exactly determined on our *Plesiadapis*

material, but it appears to be highly probable that the angle was also low in that genus, most nearly comparable to the lemurids.

The anteacetabular spine is large, but thicker and less produced outward and downward than in *Notharctus*, *Lemur*, or *Tupaia*, more like *Daubentonia* in this respect but less differentiated from the acetabular rim than in that genus.

The acetabulum is almost identical in form with that of *Tupaia* or *Lemur*. In *Daubentonia* the upper lip is much reduced.

The ischium is primitive and *Tupaia*-like in being more elongate than in any of the other comparative genera. Correlated with this is the position of the ischial spine (which is prominent, as in *Lemur* and most primitive primates) definitely posterior to the acetabulum, whereas in such later primates as have it, it is nearly above the posterior acetabular rim. In *Tupaia* it is slightly more posterior than in *Plesiadapis*. The ischial tuberosity is very slight, even less expanded than in most lemurs and definitely less than in *Notharctus*, in which it is larger than in modern lemurs, markedly unlike that of *Daubentonia*, and closely similar to the primitive condition of *Tupaia*. The inferior ramus of the ischium, although incompletely preserved, is clearly of the slender lemuroid type, much less expanded than in *Daubentonia* and slightly less than in *Tupaia* (but cf. *Ptilocercus*). It was probably directed slightly less anteriorly than in *Lemur*, and more as in *Tupaia*. The upper and anterior margins of the obturator foramen are much as in *Tupaia*, and probably the symphysis was also. This is unquestionably primitive in comparison with the slight modifications seen in *Lemur*.

What is preserved of the pubis is exactly like *Lemur* or *Tupaia*, these genera not differing significantly in this part, and noticeably less like *Daubentonia*.

Femur.—The proximal end of the femur is preserved in association with Amer. Mus. No. 17379, and there is also an isolated distal end, poorly preserved but showing the essential characters. The length is not determinable.

The head is spherical and the neck constricted, as in *Tupaia* and *Lemur* and unlike *Notharctus*. The greater trochanter extends as far as the head proximally, as in *Tupaia* (but not *Ptilocercus*); in *Ptilocercus* and *Notharctus* it does not extend so far, and in *Lemur* it extends farther. The general shape and development of the greater trochanter is very lemur-like, but the external surface is less expanded and the notch between the trochanter and the head is deeper, both primitive characters and resemblances to *Tupaia*. The intertrochanteric ridge is low and

barely visible, as in all comparable forms, and does not extend relatively as far down the shaft as in *Tupaia*, *Lemur*, or related forms.

The lesser trochanter is enormously developed, somewhat more so

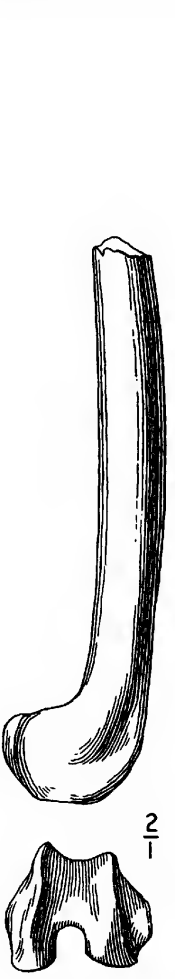

Fig. 10

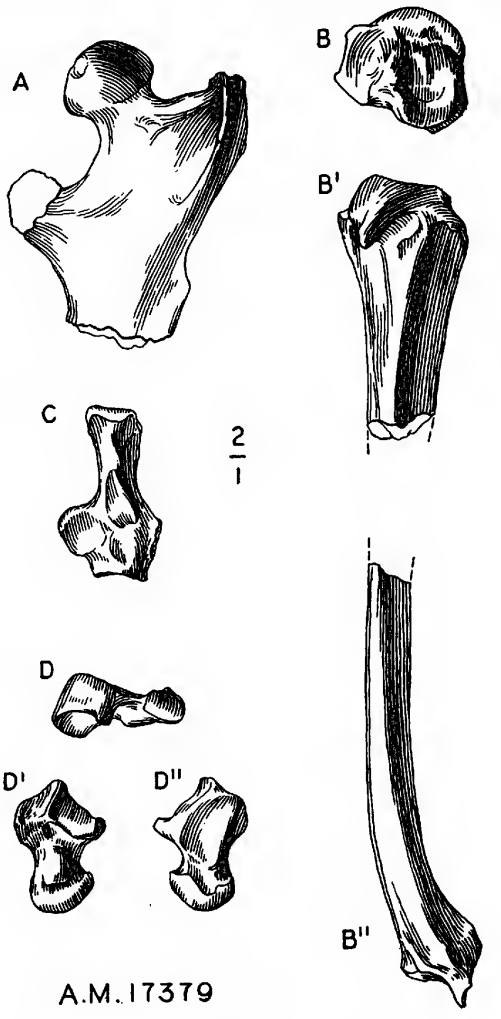

Fig. 11

Fig. 10. *Plesiadapis gidleyi*. Distal part of femur, Amer. Mus. No. 17409 (not certainly associated with pelvis of preceding figure). Lateral and distal views. Twice natural size.

Fig. 11. *Plesiadapis gidleyi*. Hind limb bones. Amer. Mus. No. 17379. A posterior view of proximal end of femur. B proximal and B′ approximately external views of proximal end of tibia. B″ posterior view of distal end of tibia. C dorsal view of calcaneum. D external, D′ plantar, and D″ dorsal views of astragalus. All twice natural size.

than in any genus with which comparison has been made, although enlargement of this process is typical of all the lower primates. It is fully internal, is directed upward and inward, and projects slightly farther than does the head of the femur. The end is rounded and is convex on the posterior and excavated on the anterior surface, somewhat as in *Lemur* in which, however, the trochanter is much smaller and is directed less upward.

A distinct third trochanter also occurs and is more elongate and thinner than in *Lemur*, more like *Tupaia*. In *Daubentonia* this process is smaller and is above the level of the lesser trochanter. In *Lemur* (and *Notharctus*) it is opposite the lesser trochanter. In *Plesiadapis* it is below the latter and in *Tupaia* is still farther down the shaft than in *Plesiadapis*. In this character, as in a number of others noted, *Tupaia-Plesiadapis-Lemur* form a progressive structural series. The most obviously distinctive character of the distal end of the femur in this series is that of the patellar groove. In *Tupaia* it is very shallow, broad, symmetrical, and sharply keeled on both sides. In *Lemur* it is narrower, deeper, and the external keel is higher and more rounded. In *Plesiadapis* it is intermediate in width, depth, and symmetry, but the external keel is as sharp as in *Tupaia*.

Tibia.—In Amer. Mus. No. 17379 proximal and distal ends of the right tibia, both slightly damaged, are present but the shaft is incomplete. There is also an isolated and imperfect right proximal end of a smaller, but conspecific, tibia. The proximal facets differ from *Lemur* in no significant respect, but the proximal part of the shaft is peculiar. The cnemial crest is weaker than in *Tupaia*, and hence more *Lemur*-like but the lower anterior tuberosity (Gregory) is either not differentiated (cf. *Tupaia*) or lower on the shaft than in *Lemur* (cf. *Notharctus*). There is, however, a definite tuberosity at this level on the internal face of the shaft, suggestive of the condition in the lorisiforms, one of the very few characters more like the lorises than like the lemurs, although even this is far from identity and is probably convergent as the loris tibia is not otherwise particularly close to *Plesiadapis*. There is a definite posteroexternal crest and also a strong posterior or posteromedian crest, originating above at the posterior margin of the medial condyle. This development of two crests, which converge on the posterior surface not far down shaft, is not seen in any of the other genera examined.

At the distal end the malleolus is produced, as in primates generally, but less than in *Lemur* and with only the slightest suggestion of the hook-like modification so characteristic of *Lemur* and many other primitive

primates. It is also less prominent and sharp than in tupaioids. The surfaces of the trochlear and malleolar facets of the astragalus meet at an open angle, considerably greater than 90°, and are not sharply differentiated.

The fibula is not preserved.

ASTRAGALUS.—The right astragalus and left calcaneum are present with Amer. Mus. No. 17379, and there is an isolated right calcaneum of the same species. This bone seems to have some, and perhaps diagnostic, basic primate characters, but is very much *sui generis*, its marked peculiarities not specifically approaching the tupaioids or any other of the groups compared. Apparently a peculiar habitus of the pes is implied, but lacking fuller evidence this cannot be elucidated.

The body is close to that of *Lemur* in general proportions, but slightly shallower (and much shallower than in *Notharctus*, which exceeds *Lemur* in this dimension). The trochlea is relatively narrow, but very shallow. The fibular crest is sharp and is more prominent than the tibial crest; in lemurs there is tendency to reverse these proportions. The tibial crest is very rounded, is in fact hardly a crest, and the angle between the trochlear and malleolar surfaces is considerably greater than 90°. The ectal facet is relatively open and is smaller than the sustentacular facet, these being rather lemuroid, as opposed specifically to tupaioid characters. The neck is notably shorter and more oblique than in either tupaioids or lemurids and the head is transverse and compressed dorsoventrally.

In view of the generally close agreement throughout other known parts of the skeleton with lemurs, tupaioids, or both, it is remarkable to find an astragalus of such divergent type in *Plesiadapis*. There can, however, be little question that the bone is correctly referred to this genus. It is of appropriate size, it articulates well with a tibia almost surely of *Plesiadapis*, it was found in apparent association with a partial skeleton of that genus, and there is no other known animal in the fauna to which it could belong with reasonable probability. Some characters suggest other orders, but the general character is not incompatable with primate relationships and the plantar facets are very lemur-like. The astragalus is too peculiar to give decisive evidence of relationship, but would not contradict a hypothesis, strongly based on other evidence, of divergence from an early lemuroid stock.

Teilhard has shown that the astragalus figured by Lemoine as of *Plesiadapis* (1892, Pl. x, fig. 13) is really of *Pleuraspidotherium*, and that

supposed to be of *Platychoerops* ("*Plesiadapis*" *daubrei*, Lemoine, 1892, Pl. x, fig. 14) is probably also erroneously identified and too imperfect to be of value.

CALCANEUM.—The proximal end of the calcaneum and the ectal facet are almost as in *Lemur*. The perineal tubercle is well developed (cf. *Tupaia*), and the sustentaculum is short but strong. The bone ends almost immediately distal to the sustentaculum. The cuboid facet is concave and nearly circular. If the *Lemur* calcaneum had the portion distal to the sustentaculum abbreviated, it would closely resemble that of *Plesiadapis*. It is interesting that this structural change (in reverse order) does seem to have occurred. In *Notharctus* this distal portion is shorter than in *Lemur*, and in *Pelycodus* shorter than in *Notharctus*. In *Adapis*, presumably conservative in this respect, it is nearly as short as in *Plesiadapis*. *Plesiadapis*, however, evidently was not definitely beginning the lemuroid foot specialization, even to the extent that *Tupaia* has done so, but was following a line of its own.

The calcaneum figured by Lemoine (1892, Pl. IX, fig. 16), as of *Orthaspidotherium* or *Plesiadapis* is sufficiently similar to the present specimen to be of the latter genus, but the figure is not characteristic enough to make the determination certain.

PHALANX.—A phalanx probably of the pes but indeterminable, is in probable association with Amer. Mus. No. 17379. It is shorter and stouter than the metacarpal described above. The proximal articulation faces backward and slightly upward and is smoothly concave, with a notch between the tuberosities below. The shaft is arched, and has lateral plantar ridges rising into low prominences near the distal end. The distal articulation is almost entirely on the plantar side and is in the form of half a transverse cylinder divided, however, by two grooves into three longitudinal ridges.[1]

Among the many isolated bones from the Mason Pocket is another phalanx of this type, and several of a different type which may, nevertheless, also (or instead of that described) belong to *Plesiadapis*. These have the proximal facets concave only in the dorso-plantar direction, the shafts without ridges, and the distal facets pulley-like and extending well up onto the dorsal surface.

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[1] Lemoine (1892, Pl. IX, fig. 28) referred a very similar phalanx from the Cernaysian to *Plesiadapis*.

AFFINITIES[1]

A number of varied genera, *Apatemys*, *Stehlinella*, *Heterohyus*, and others, were formerly considered as relatives of *Plesiadapis* and placed in the Plesiadapidae, but Jepsen (1934) has recently sorted out this heterogeneous assemblage, placing the genera mentioned and several others in the Apatemyidae. The relationships of the Apatemyidae are not necessarily, or probably, the same as those of the Plesiadapidae and are not here under discussion. The family Plesiadapidae is a distinctive unit, essentially as redefined by Jepsen, including the genera *Pronothodectes* Gidley, *Plesiadapis* Gervais, *Chiromyoides* Stehlin, and *Platychoerops* Charlesworth.[2] For present purposes it may be assumed that these genera are related to *Plesiadapis* as its only recognizable immediate allies, and only broader relationships will be discussed.

Lemoine's opinion is not very explicit from the point of view of modern taxonomy, but he spoke of *Plesiadapis* as being "lémurien" or as having "des caractères lémuriens avec un facies marsupial" (1887).[3] Schlosser at first accepted Lemoine's reference to (or rather comparison with) primates, but later (1892) considered the genus as a rodent, then (1911) as an insectivore, and finally (1923) returned to belief in primate and now in definitely "chiromyiform," affinities. Forsyth Major (1899) considered it as a rodent or duplicidentate. Matthew (e. g., 1914), before he had studied the genus at first hand, referred it to the Insectivora. Stehlin (1916) considered the primate affinities of *Plesiadapis* as beyond any question, and somewhat more tentatively considered it as especially related to "*Chiromys*" (*Daubentonia*). This was accepted by Teilhard (1921) and, largely on the authority of Stehlin and Teilhard, by almost all other students, especially in Europe. It is much the most widespread view in recent literature.

On examining part of the present material, however, Matthew (1917) pointed out the weakness of Stehlin's argument, especially as regards special affinities to *Daubentonia*. He reserved judgment until the skeletal material could be studied (which unfortunately he never was able to carry out), but in the meantime stated tentatively that the

[1] It is impossible to approach the study of an animal as widely known and as much discussed as *Plesiadapis* without having already formed some opinion, however tentative, as to its affinities, and this prejudgment must unconsciously color the emphasis and interpretation of evidence. It should therefore be noted that on starting this study I believed *Plesiadapis* to be perhaps related to *Daubentonia*, as Stehlin believed, or an offshoot of the early tarsioids, as its primate-like character and association with tarsioids, before the appearance of known lemuroids, might suggest. The fact that the conclusion reached is decidedly different is, of course, no guarantee that this conclusion is correct, but it does show it to be free from bias.

[2] Jepsen also places *Plesiolestes* here, but I think it extraneous, and he considers *Platychoerops* as a synonym of *Plesiadapis* while I hold it to be distinguishable generically. These points will be discussed elsewhere.

[3] He had also earlier compared *Plesiadapis* with "*Chiromys*," thus anticipating Stehlin (as the latter notes), but apparently he abandoned this comparison.

evidence then before him "suggests that it is a very primitive primate," making no suggestion as to closer affinities. Gregory (1920), however, has more persistently clung to Matthew's and his earlier view that *Plesiadapis* is an insectivore allied to the tupaioids,[1] stating that the humerus gives evidence to this effect which is strengthened by that from many other parts of the skeleton [that described above].

Gidley (1923) pointed out that there are some distinctive dental characters among early primates which are readily recognizable and which do not appear to occur in any other order, and that while some molar types are very equivocal others seem to be infallibly diagnostic of the Primates. He further stated that *Plesiadapis* ("*Nothodectes*") has such a diagnostic molar pattern and is therefore a primate, with little doubt. Comparison was made especially with notharctines and the less specialized platyrrhines.

The general questions thus raised by the various opinions so far expressed[2] are thus:

1. Whether it is a primate by definition or is not rather an earlier offshoot of the group of Insectivora from which the primates arose.
2. Whether, if it is definitely primate, it is related or ancestral to *Daubentonia*.
3. If primate but not near *Daubentonia*, whether it shows special relationship to any other major group, with special reference to the tarsioids and lemuroids.

Anticipating the conclusions reached below, on present evidence I believe:

1. That *Plesiadapis* is definitely to be classed as a primate.
2. That it shows no valid evidence of any special relationship to *Daubentonia*.
3. That it does show strong evidence of relationship to the tupaioids on one hand and the lemuroids (adapids and Malagasy lemurs) on the other, evidence most reasonably interpreted by considering *Plesiadapis* a derivative of the lemur ancestry not long after its divergence from that of the tupaioids. It is a sterile branch not more closely related to any known later primates.

In considering these problems, comparison has been made especially with *Tupaia* (also *Ptilocercus*), *Lemur* (and other lemurids, especially *Myoxicebus*), *Loris*, *Nycticebus*, and some other non-Malagasy primitive primates, *Notharctus*, *Tarsius*, and *Daubentonia*. Other genera were also compared, but these adequately represent the groups necessary to consider and serve to present the evidence. Explicit comparison with platyrrhines and catarrhines proved to be unnecessary after a preliminary trial,

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[1] I. e., "Menotyphla" in his text, but the group Menotyphla is now believed to be unnatural in this sense and is not based on *Tupaia* and its true allies, with which Gregory's comparison is primarily made.

[2] The view of Schlosser (later abandoned) and of Forsyth Major that *Plesiadapis* is a rodent seems so manifestly controverted by its whole structure and has been so adequately discussed by Stehlin as to require no further notice.

as these more advanced forms show no especial resemblance to *Plesiadapis* not also shown by lemuroids.

The question of primate or insectivore relationships has become one purely of primate or tupaioid affinities, as there is no question of close resemblance to any insectivores other than the tupaioids.[1] Since the tupaioids are now universally recognized as a conservative offshoot of the primate ancestry, the plesiadapids are related to the primates in either case, and the question as to their inclusion in that order or in a protoprimate division of the Insectivora is in part purely verbal. In fact it ceases to exist at all if Le Gros Clark (1934) is followed in placing the tupaioids in the Primates, and his evidence is so detailed, so carefully evaluated, and so convincing that I see no reasonable alternative to such a course. If the tupaioids are primates, then the plesiadapids are necessarily primates also. The essential point, however, as to whether they are closer to tupaioids or to some other group among the primates, remains.

The evidence of the dentition has not been very fully analyzed. Most students have called it vaguely "lemuroid." Stehlin (1916) emphasized the *Daubentonia*-like enlargement of the incisors, but he noted that these are functionally quite different from those of *Daubentonia*, with which they could only be linked by intermediate forms testifying to the reality of the profound changes involved. Such intermediate forms he thought recognizable in *Chiromyoides* and *Heterohyus* (*Amphichiromys*, *Heterochiromys*). But later discovery and research (culminating and summed up in Jepsen, 1934) have clearly shown that *Chiromyoides* is barely separable from *Plesiadapis* and makes only the most distant and superficial approach to *Heterohyus*, while the structural ancestry of *Heterohyus* can be traced back to *Labidolemur*, which is contemporary with *Plesiadapis* and even at that early date clearly belongs to quite a different line of development. As regards the cheek teeth, those of *Daubentonia* are so degenerate that they show little more than that they were probably derived from a tuberculosectorial type. As all Eocene and Paleocene primates (and most other earliest Tertiary mammals) are of this type, the positive evidence is wholly inconclusive. Stehlin points out that they could be derived from *Plesiadapis*, but this is negative evidence of no particular value. They could about equally well be derived from any other Paleocene or Eocene primate, or for that matter from any one of many insectivores, rodents, carnivores, or even ungulates, as far as this evidence goes.

[1] Matthew (1917) pointed out certain analogies to soricoids in the dentition, but did so only descriptively. He never maintained that any special soricoid relationship is indicated.

Stehlin's argument may perhaps be summed up as being that *Daubentonia* must somewhere on earth have had as a basal Tertiary ancestor a primate with enlarged incisors, that *Plesiadapis* is a basal Tertiary primate with enlarged incisors, and that therefore *Plesiadapis* is or may be the ancestor of *Daubentonia*.[1] Every point is, however, dubious in the extreme. It is possible, but conjectural, that *Daubentonia*'s enlarged incisors date from the Paleocene. Nothing is known of the date of origin or rate of acceleration of this character. Such characters can be developed rapidly. Analogy with rodents does not appear to have much bearing and even they probably developed rootless incisors rapidly. Although this occurred in them before the Eocene, it may have occured in *Daubentonia* at the same rate but at a different time, the Pliocene for instance. Nothing is actually known as to this. On the second point, *Plesiadapis* is not the only early primate with enlarged incisors. These developed at least six times in the Paleocene and Eocene. *Tetonius*, *Necrolemur*, *Carpolestes*, *Labidolemur*, *Phenacolemur*, and *Plesiadapis* (and allied genera in each case) represent different lines of descent in each of which enlarged front teeth apparently developed independently. As the lines are divergent, it is unreasonable to suppose that more than one of them is related to *Daubentonia*. It is, furthermore, unnecessary and in fact impossible to assume a priori that any of them is related to *Daubentonia*, the early Tertiary history of which is quite as likely to be unknown as is its later history. A conclusion cannot be reached with any probability except on better evidence than mere enlargement of anterior teeth, an adaptive character which has appeared over and over again in many different groups of mammals.

As regards molar pattern, *Plesiadapis* resembles the primitive Notharctinae more closely than any other group. The resemblance to the Adapinae is more distant, but still striking in many respects. There is also considerable resemblance to *Necrolemur*, a later tarsioid, and to *Paromomys*, a Middle Paleocene genus of doubtful position perhaps tarsioid. Resemblance to the other main groups of early primates is more distant.

The resemblance to *Pelycodus*, most primitive known notharctine, is really amazing and extends to the apparently most insignificant details. The upper molars are of almost identical structure throughout, differing only in details of the cingula and proportions such as may characterize species of one genus. In the lower molars, *Pelycodus* has the

[1] It is impossible and unnecessary to repeat the argument in full, but it is perhaps unjust to abbreviate it without adding that Stehlin's views are presented logically and with proper caution and that his whole discussion, even though in part superseded by later discovery, marked a great stride forward.

paraconids slightly more distinct, but the resemblance is equally striking and includes even such features as the minute grooving of the trigonid face of the metaconid and the exact structure of the complex grooving of the talonid face of the hypoconid and of the whole heel of M_3. Matthew and others have noted this resemblance, although hardly recognizing its very complete character, but have tended to distrust or even reject it because of the well-known fact that early tuberculosectorial dentitions are all more or less alike and that erroneous allocations have frequently resulted from comparisons of molar teeth alone. This, is, of course, true, but it is also true, as Gidley pointed out, that such complete convergence in a really complicated pattern as occurs between *Plesiadapis* and *Pelycodus* has rarely or never been found in mammals not truly related, and that the characteristic structure of *Plesiadapis* molars is encountered in no order other than the Primates. The evidence of molar pattern is decidedly in favor of rather close relationship to the Notharctinae. As this happens to be correlated with other resemblances to that subfamily or, more broadly, to the general division of primates which it represents, there is every reason to accept this evidence as valid.

$P\frac{3-4}{3-4}$ are decidedly less notharctine. P^{3-4} are variable in both groups, and may be closely similar. The most obvious difference in some species of *Plesiadapis* is the large conule, but this is reduced or absent in the more advanced species of *Plesiadapis* and in its close ally *Platychoerops* (that is, in the forms actually contemporaneous with the notharctines available for comparison). P_{3-4} show that the two groups are divergent (which is obvious in any event) but offer no evidence for or against relationship. In *Plesiadapis* these teeth are relatively short and broad, in *Pelycodus* generally more slender. The trigonid is more highly differentiated in *Pelycodus*, but this is a progressive character approached by the more advanced plesiadapids.

The anterior teeth are, of course, very unlike in the two groups. The very doubtful suggestion of possible tarsioid affinities in the dentition consisting of a resemblance (much less exact than to the Notharctinae) in the posterior teeth to a few advanced and aberrant later fossil tarsioids and to some doubtfully placed early genera, is negatived by the known skeletal characters. In all the characters in which *Tarsius* differs from the lemuroids and which are known in *Plesiadapis*, the latter is nearer the lemuroids. Nor does it show any of the definite, but in some cases rudimentary, tarsioid developments also to be seen in only slightly later fossil tarsioids. It is hardly possible that the plesiadapids have any closer

relationship to the tarsioids than implied in the statement that both are primitive primates.

A similar conclusion seems to be even more strikingly, and rather surprisingly, true as regards *Daubentonia*. I am unable to find any characteristic daubentoniid character, even in the most rudimentary form, in any known part of *Plesiadapis* beyond the enlarged incisors, which are not really very similar and have little or no value as evidence, as pointed out above. If the ancestry of *Daubentonia* really had already begun to diverge in the Paleocene and was already characterized by enlarged incisors, it is reasonable to suppose that it would also have some other daubentoniid characters, among the many which appear in the whole skeletal structure, but *Plesiadapis* has none. If, as is also possible, *Daubentonia* is really a more modern offshoot of the general lemurid stock, this would necessarily imply that its early Tertiary lemurid ancestry was more generalized than is *Plesiadapis*. In short, there is no evidence that *Plesiadapis* is related to *Daubentonia*, there is much evidence that it is not so related, and this view can no longer be maintained.

It is still possible that *Daubentonia* is related to the Apatemyidae, although the evidence is very inadequate and not very convincing. The question is foreign to the present discussion.

Plesiadapis does show numerous and striking resemblances to three groups: Adapidae, Tupaiidae, and Lemuridae. Special relationship with all three is entirely possible. Gregory[1] (1920) has conclusively shown that the adapids are a primitive offshoot of the lemuroid ancestry. Le Gros Clark (1934) has similarly demonstrated that the tupaioids are a still more primitive, more persistent, but more conservative offshoot of the same stock. The dentition is aberrant in the diprotodont habitus, notharctine in molar structure, apparently somewhat less lemurid and much more notharctine than tupaioid.

The skeletal characteristics, explicitly brought out in the comparative description above, may be summarized as follows:

1. Most of the many characters shared by tupaioids and lemuroids are also present in *Plesiadapis*. These characters define the whole tupaioid-notharctine-lemurid line, and show that *Plesiadapis* is a member or a derivative of this series.

[1] Gidley (1923) very sharply attacked Gregory's conclusion. His arguments are principally (a) that the Adapidae (or Northarctinae) are not lemuroids because they resemble only the Malagasy, not the African and Asiatic "lemurs," and (b) that they are platyrrhines because they resemble that group in many characters. Both these points were even more fully brought out by Gregory and were, it would seem, more logically interpreted by him. The first suggests that the Adapidae and Malagasy lemurs belong to a natural group from which the lorisiforms are excluded, which is the conclusion reached by Gregory long before. The second suggests that the Adapidae, or Notharctinae, stand near the platyrrhine ancestry, which was also Gregory's conclusion. Whether they be considered as pre-platyrrhine lemuroids (Gregory) or as lemuroid platyrrhines (Gidley) does not really seem to be as important or as different as Gidley suggests, but the former seems somewhat more in accord with the evidence and more conducive to a broad view of relationships.

2. In many characters *Plesiadapis* is definitely closer to the notharctines, lemurids, or both than to the tupaioids. Individual characters of this sort are not very conclusive, but so many are found, in almost all parts of the skeleton, that it seems highly probable that they are significant. They show that the plesiadapids branched off from the lemurid stock after the separation of the more primitive tupaioids.

3. There are a few characters in which *Plesiadapis* resembles the tupaioids rather than the lemurids, and more (but still fewer than in the second category) in which it is approximately intermediate between the tupaioids and lemurids. As far as can be judged, these are without exception characters in which the tupaioids are archetypal to the lemurids, and they therefore suggest merely that when the plesiadapids arose from it the lemurid ancestry still retained certain primitive features which were lost in later forms.

4. There are one or two characters in which *Plesiadapis* resembles the lorisiforms more than the lemuriforms but these are so few, the resemblance is so inexact, and the characters are so unimportant and easily convergent in nature that they can hardly indicate any special relationship. The plesiadapid structure is lemuriform, and not lorisiform, throughout.

5. *Plesiadapis* has several specifically notharctine characters, especially in the molar pattern but also a few in the skeleton. It also has a few specifically lemurid characters, or characters of the general lemuroid ancestry retained in lemurids and lost in notharctines. The suggestion is that the plesiadapids arose from the primitive lemuroid ancestry at about the same time as the notharctines and probably from the same subdivision or general stock as the latter. They can hardly, however, have arisen from a differentiated and specifically notharctine ancestry.

6. There are numerous characters in which *Plesiadapis* is divergent from all the other groups mentioned. These are the characters of the plesiadapid line as such and are in general adapative habitus characters, not wholly concealing more basic resemblances. They show that the plesiadapids were an early side line, specialized in its own way, not ancestral to any known forms.

The following suggested new classification of the Suborder Lemuroidea involves the conclusions of the present study, and also a detailed review of the whole subject, with special reference to the recent work of Le Gros Clark (summed up in 1934).[1]

The form and the abbreviations are as in my general classification of mammals (1931), and this may be taken as superceding the classification of the same suborder on page 271 of that paper.

1. Suborder LEMUROIDEA Mivart, 1864.
   Infraorder LEMURIFORMES Gregory, 1915.
   Superfamily Tupaioidea
   †Fam. Anagalidae Simpson, 1931. Olig.; As.
   Fam. Tupaiidae Mivart, 1868 (Tupaina Gray,1825; Tupaiadae Bell, 1839). R.; As.

[1] I am personally indebted to Professor Le Gros Clark for additional comments and for examining this classification, for the imperfections of which, however, he is not responsible and which he has not seen since the Plesiadapidae were removed from the Daubentonioidea and placed in the Superfamily Lemuroidea.

Superfamily Lemuroidea

†Fam. Plesiadapidae Trouessart, 1897. M. Paleoc.-Eoc.; N.A., Eu.

†Fam. Adapidae Trouessart, 1879. [Including Notharctidae Trouessart, 1879]. Eoc.; Eu., N.A.

Fam. Lemuridae Gray, 1821. [Including Megaladapidae Forsyth Major, 1893, Nesopithecidae Forsyth Major, 1896.] Pleist.-R.; Madagascar.

Fam. Indridae Burnett, 1828 (Indrisidae Alston, 1878.) R.; Madagascar.

Superfamily Daubentonioidea

Fam. Daubentoniidae Gray, 1870 (Daubentoniadae Gray, 1863 = Cheiromydae Gray, 1821, invalid name). R.; Madagascar.

Infraorder LORISIFORMES Gregory, 1915.

Fam. Loridae Gray, 1821. ?Plioc.-R.; S. As.

R.; S. As.

Fam. Galaginidae Alston, 1878 (Galagonina Gray, 1825). R.; Af.